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**Catalogue and Review  
of the Type Fossil Crocodilians  
in the Yale Peabody Museum**

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Glenn W. Storrs**

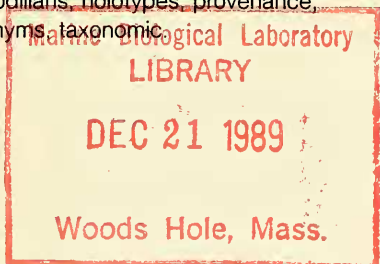
(Received 7 April 1988)

**Abstract**

A systematic review of fossil crocodilian holotypes in the Yale Peabody Museum provides a basis for taxonomic reinterpretation of the specimens. Several species are rejected as having been erected upon indeterminate material or as being junior synonyms of existing taxa. For valid taxa, new descriptions, designations, and/or diagnoses supplement the originals when necessary. Several fossils have received clarification of their provenance data.

**Key Words**

Crocodilians, holotypes, provenance,  
synonyms, taxonomic



**Introduction**

*It is certainly true that everyone who does original work in systematic zoology, either among the living or extinct forms, meets many difficulties at the start in endeavoring to ascertain what others have done before him. The literature of the subject is often discouraging from its extent, and especially from its uncertainty. If work at hand requires the comparison of type specimens, the difficulties greatly increase, and often prevent definite conclusions. The type will frequently be found the most important element in the problem, far more so than the literature, however extensive.*

*In the choice of specimens worthy of being types, I can only suggest a course that seems to me the proper one. I believe experience has already shown that to make types of incomplete or uncharacteristic specimens is seldom of permanent advantage to an author, and almost always a lasting injury to the branch of science he represents.*

O. C. Marsh, 1898

During the past few years the Vertebrate Paleontology Collection of the Yale Peabody Museum of Natural History has undergone extensive reorganization. This project, coupled with the addition of the Princeton University fossil vertebrate collection in 1985 and its subsequent reorganization, has greatly enhanced the accessibility and scientific usefulness of all specimens. However, during

recuration it became apparent that significant inconsistencies often exist between original descriptions of material and the corresponding specimens found in the collection. Questions can be raised concerning the provenance and affinities of many specimens. These problems stem from several factors, ranging from original descriptions and data statements that are now known to be inadequate or inaccurate to specimen loss and/or damage. This situation is particularly acute among the type specimens of certain fossil crocodylians. This report provides an up-to-date summary of the available information for each holotype specimen of fossil crocodylian in the Yale Peabody Museum (YPM). Indeed, Recommendation 72 G of the International Commission on Zoological Nomenclature (Ride et al. 1985) suggests that it is the responsibility of each repository to publish a list of the type material in its possession or custody. Recent work on the morphology and systematics of crocodylians provides a sound basis for this review. It is hoped that as curation continues, summaries for other groups of Yale type specimens will also become available.

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### Systematic and Nomenclatural Procedures

For the sake of continuity and practicality we have tried, in every case, to alter the existing nomenclatural conventions for the concerned taxa as little as possible. However, where taxa had previously been inadequately diagnosed, some nomenclatural revisions have been necessary. A difficulty in this undertaking is that, with the exception of Clark's recent work (1986), no truly phylogenetic analysis of crocodylians has been completed and specific diagnoses based upon a hierarchic distribution of characters have not always been possible. The original type names and subsequently published revisions are arranged below alphabetically along with discussions of their status and new descriptions where necessary. With regard to the genus

*Crocodylus*, original citations often used the archaic spelling (and junior synonym) *Crocodylus*. Our first reference to each such occurrence uses the original spelling unaltered. Thereafter, archaic spellings appear in quotes until reassigned to *Crocodylus*. A brief summary of taxonomic changes follows the reassessment of the fossils.

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### Abbreviations

AMNH American Museum of Natural History (New York)  
YPM Yale Peabody Museum of Natural History (New Haven)

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### Taxa of Interest

#### *Crocodylus affinis* Marsh, 1871a

**Holotype** YPM 1345.

**Accession Number** 133.

**Catalogue Entry Date** 25 January 1910 (Marsh's original catalogue listed no entry dates for his specimens. In such cases, the date represents the time at which the entry was transferred to the current catalogue).

**Horizon** Eocene (Lutetian, Bridgerian), Bridger Formation, probably Bridger B of Matthew (1909) (upper Black's Fork Member).

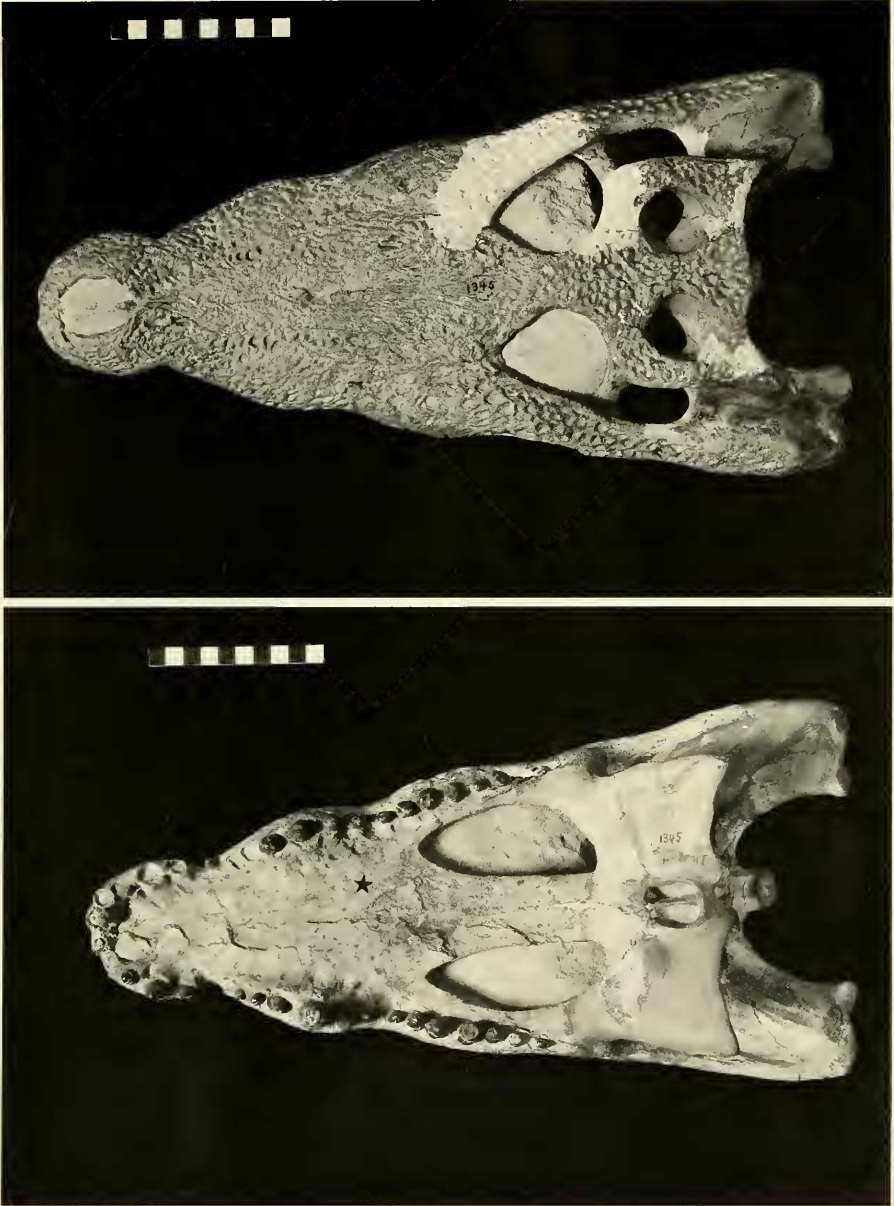
**Locality** Grizzly Buttes, near Fort Bridger, probably in Sec. 28, T14N, R115W, Bridger Basin, Uinta County, Wyoming.

**Collectors** O. C. Marsh, H. D. Ziegler, A. H. Ewing, E. Whitney; Yale College Scientific Expedition, 1870.

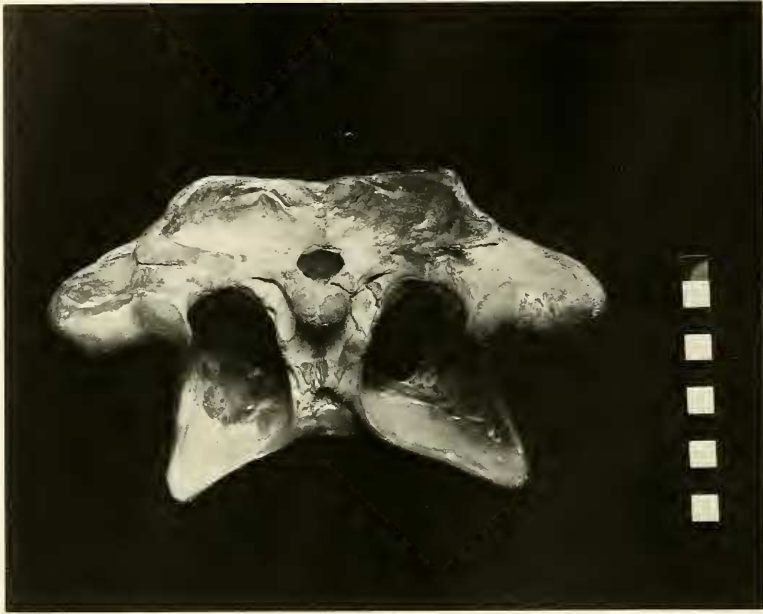
**Material** A well-preserved skull and mandible (Figs. 1, 2).

**Remarks** Although *Crocodylus* [sic] *affinis* is represented by exceptional material, detailed discussion of its anatomy relative to its

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**Fig. 1**  
Top) *Crocodylus affinis*, holotype, YPM 1345, dorsal  
aspect, scale in centimeters; bottom) same  
specimen, ventral aspect.



**Fig. 2**  
*Crocodylus affinis*, holotype, YPM 1345, occipital  
aspect, scale in centimeters.

phylogenetic position is difficult since few fine details of phylogenetic significance are preserved, limiting comparisons with extant forms.

Marsh's (1871a) original description of the type material was augmented by Cope (1884), who referred additional specimens to the taxon. Troxell (1925a), in an early review of the Peabody crocodylians, attempted to include a comparative description but was hampered by a lack of comparative material. Troxell's (1925a) analysis failed to discuss specific similarities between taxa, but rather concentrated on elucidating minor differences in cranial proportions, and determined little more than that '*C. affinis*' was not an alligatorid. In light of the then prevailing systematic philosophy, he therefore considered the fossil a crocodylid.

'*Crocodylus affinis*' exhibits a number of primitive features of the Crocodylia. These include a transfrontal ridge (spectacle) anterior to the orbits and a large basisphenoid

contribution to the lateral wall of the braincase. Unfortunately, the splenials are not preserved, and indication of a possible foramen intermandibularis oralis is therefore lacking. The posterior angle of the lateral temporal fenestra was apparently formed by the quadratojugal, although poor preservation in this region prohibits definitive examination. The quadratojugal has an extensive dorsal surface lateral to the quadrate's articular condyle. A small supraoccipital is present on the parietal table. The postorbital of '*C. affinis*' is relatively narrow. Laterally, the postorbital is shielded from the edge of the parietal table by a hornlike anterior process of the squamosal. The external nares are large and anteriorly oriented.

Interesting features of '*C. affinis*' are found in the posterior part of the mandible (Fig. 3). The retroarticular fossa on the dorsal surface of the retroarticular process is bipartite, divided along its center by a longitudinal ridge, and the lateral margin of the fossa is

depressed as in crocodyloids. The surangular participates in and extends caudad to the articular fossa, and is widely exposed anteriorly. The articular fossa is also divided; its medial portion is small and extends farther anteriorly than does the lateral part. Ventrally, the articular is abruptly terminated posteroventral to the mandibular fenestra. Anteriorly, the mandibular symphysis is long, extending caudad to the sixth dentary tooth.

The need for extensive revision of the Bridger Crocodylia was recognized by Mook (1933) and Troxell (1925a). At least six crocodylian genera and several species have been reported from the Middle Eocene Bridger Formation of Wyoming (see, e.g., Langston 1975; Mook 1921a, 1941, 1960, 1962; Norell 1988; Steel 1973; Wassersug and Hecht 1967; etc.). Some of these taxa are known from well-preserved material and represent distinct taxa, such as '*Crocodylus acer* Cope 1882 and *Brachyuranochampsa zangerli* Mook 1962. Other material is very fragmentary. Some taxa are based upon cranial proportions and other subjective size criteria, without careful scrutiny of homologous features in extant taxa or in ontogenetic series.

Our analysis of the Bridger type specimens in the Yale Peabody Museum indicates that only a few represent demonstrably distinct taxa. One of these, *Pristichampsus vorax* (Troxell 1925a) is discussed below. The taxa '*Crocodylus affinis*', '*Crocodylus brevicollis* Marsh 1871a, '*Crocodylus grinnelli* Marsh 1871a (including '*C. grinnelli herpichanus* Troxell 1925a), and '*Crocodylus liodon* Marsh 1871a, are referable to a single taxon for which the specific name *affinis* is retained. '*Crocodylus elliotti* Leidy 1870, which is also known from the Bridger beds and is similar dentally, holds nomenclatural precedence to '*C. affinis*. The extremely fragmentary nature of '*C. elliotti*, however, makes it unsatisfactory as the basis for such a ubiquitous form.

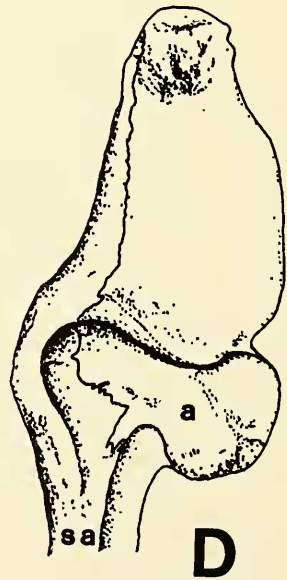
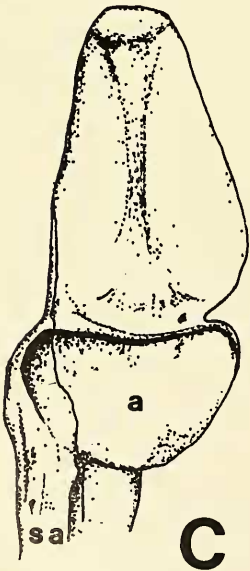
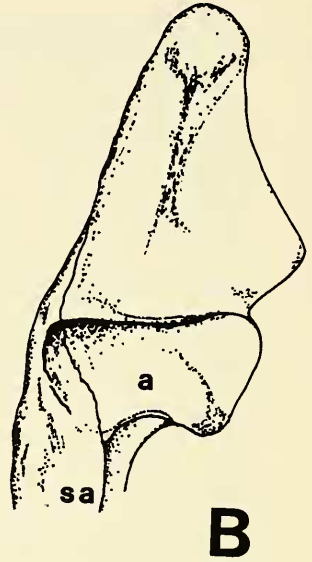
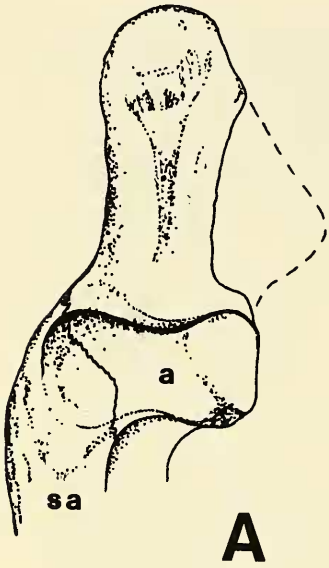
'*Crocodylus affinis* represents the most common crocodile in the Bridger beds (Cope 1884), and was a large flat-headed crocodylian with large bulbous posterior teeth resembling large extant *Crocodylus niloticus*.

Additional material was referred to '*C. affinis* by Mook (1921b). One such specimen (AMNH 6177) displays the crocodyloid (sensu Norell, in press) synapomorphy of a lost foramen intermandibularis oralis. Other skulls in the Peabody collection, comprising subadult (YPM 246) and large adult specimens (YPM 245, 258, 1352, and an uncatalogued Princeton specimen), are also referable to this taxon, as is the mandibular material (YPM 250 and 251). All of these specimens are from the Bridger Eocene of Wyoming. The referred material indicates the presence of a large quadratojugal spine as in living *Crocodylus* and *Tomistoma*.

Referral of YPM 1345 to the extant genus *Crocodylus Laurenti* 1768 (= *Crocodylus Bonnaterra* 1789) is problematic because no unique shared features are evident. However, in light of at least one crocodyloid synapomorphy (the lost intermandibular foramen of the comparative material), the designation '*Crocodylus*' (i.e., *Crocodylus*) is tentatively retained for this taxon.

The Bridger Formation is a thick fluvial sequence representing a myriad of aquatic environments, including not only stream systems but also marshes, ponds, and of course flood plains. The sediments consist primarily of a series of grey and green mudstones and sandstones and, while waterlain, contain a very large percentage of transported volcanoclastics derived from surrounding regions. The character of these rocks combined with the often abundant remains of crocodiles, as well as turtles, fish and freshwater invertebrates, suggests a warm, wet depositional basin (Matthew 1909; McGrew and Sullivan 1970; West 1976).

The first stratigraphic study of the Bridger was that of Matthew (1909) who divided the formation into five subunits. These, lettered bottom to top as A to E, were further subdivided by numerical designations. Wood (1934) later described a lower, Black's Fork Member and an upper, Twin Buttes Member corresponding to Matthew's (1909) A/B and C/D, respectively. The prolific Grizzly Buttes locality lies in Bridger B. The discussions and maps of Matthew (1909), and more recent



work by West (1976), are helpful in identifying the classic Bridger localities, but not all of Marsh's sites can be relocated.

**Diagnosis** *Crocodylus affinis* Marsh, 1871a. A medium-sized crocodilian, referable to the extant Crocodylia (sensu Clark 1986) on the basis of procoelous vertebrae and choanae bordered entirely by the pterygoids. *C. affinis* is distinguishable by the retention of the primitive features of a spectacle, a quadratojugal spine, infratemporal (subtemporal) fenestrae bordered posteroventrally by the quadratojugal, and a basisphenoid which contributes to the braincase wall and which is dorsoventrally elongate yet not laterally expanded ventral to the otoccipitals. *C. affinis* possesses the unusual derived features of a postorbital separated from the lateral skull border by an anterior process of the squamosal, and a short anteroventral ramus of the articular that terminates in a knob rather than tapering to a point.

***Crocodylus brevicollis* Marsh, 1871a**

**Holotype** YPM 1349.

**Accession Number** (?) 249+.

**Catalogue Entry Date** 25 January 1910.

**Horizon** Eocene (Lutetian, Bridgerian), Bridger Formation, probably Bridger B of Matthew (1909) (upper Black's Fork Member).

**Locality** Grizzly Buttes, near Fort Bridger, probably in Sec. 28, T14N, R115W, Bridger Basin, Uinta County, Wyoming.

**Collector** A. H. Ewing, Yale College Scientific Expedition, 1870.

**Material** Three cervical vertebrae, including the axis with fused atlas (odontoid) and three dorsal vertebrae.

**Remarks** This fossil was summarily described by Marsh (1871a) and later figured with little comment by Troxell (1925a). The procoelous centra are typical of eusuchian crocodiles (sensu Clark 1986). As eusuchian vertebrae are relatively consistent in form between taxa, the assignment of the material to *Crocodylus* ('*Crocodylus*') is problematic. The elongate ventral pits on the centra and the bifurcated hypapophyses noted by Marsh (1871a) and Troxell (1925a) are unusual, but also appear in the type specimen of '*Crocodylus*' *grinnelli* which we have synonymized with *C. affinis* (see below and above). We therefore regard '*C.*' *brevicollis* as provisionally referable to *C. affinis*. The curious character of the vertebrae does not appear to be related to a pathologic condition and may be characteristic of *C. affinis*, although postcranial remains are not associated with the type skull.

***Crocodylus grinnelli* Marsh, 1871a**

**Holotype** YPM 1344.

**Accession Number** 129.

**Catalogue Entry Date** 25 January 1910.

**Horizon** Eocene (Lutetian, Bridgerian) Bridger Formation.

**Locality** Marsh's Fork, Bridger Basin, Wyoming.

**Collector** G. B. Grinnell, Yale College Scientific Expedition, 1870.

**Material** A fragmentary skeleton and skull including quadrates, frontal, basioccipital, and mandibular and rostral fragments. Several

◀ **Fig. 3**

Right articular and retroarticular fossae of: A, *Crocodylus affinis*, holotype, YPM 1345, dorsal aspect; B, *Crocodylus niloticus*; C, *Alligator mississippiensis*; D, *Caiman jacare*. Anterior to bottom, drawings not to scale, a—articular, sa—surangular.

fragmentary postcranial elements are also present.

**Remarks** The preserved elements of '*C.*' *grinnelli* are indistinguishable from their counterparts in the type specimen of *C. affinis*. The cranial elements display the preorbital spectacle, a medial crest on the ventral surface of the quadrate, an anterior process of the squamosal along the lateral border of the postorbital, and an elongate, unexpanded basioccipital. The mandibular fragments exhibit the peculiar mosaic of bones forming the articular fossa, with a large participation of the surangular, the bipartite division of the retroarticular process, and the short anteroventral ramus of the articular. As no distinguishing characteristics are obvious in the type material of '*C.*' *grinnelli* we consider it a junior synonym of *C. affinis*.

***Crocodylus grinnelli herpichanus* Troxell, 1925a**

**Holotype** YPM 300.

**Accession Number** 3544.

**Catalogue Entry Date** 16 September 1926.

**Horizon** Eocene (Lutetian, Bridgerian) Bridger Formation, horizon B5 of Matthew (1909) (uppermost Black's Fork Member).

**Locality** Sage Creek, "in a pocket south of the broad butte," Bridger Basin, Uinta County, Wyoming.

**Collector** E. L. Troxell, August 1922.

**Material** A very complete skull and skeleton. The skull has been flattened dorsoventrally.

**Remarks** This specimen is adequately described by Troxell (1925a). Its completeness provides a sound basis for an understanding of the postcranial characteristics of the taxon. Apparently, however, the specimen was given

a subspecific name more out of Troxell's admiration for his preparator, Fred Herpich, and the complete preservation of the fossil than for its morphological uniqueness. Later, Troxell (1925b) referred to this skeleton as a distinct species but without further qualification. Differences between YPM 300 and an expanded concept of *C. affinis* are within the range of variation seen in extant crocodylians. Therefore, '*C.*' *g. herpichanus* is a subjective junior synonym of *C. affinis*.

***Crocodylus hartti* Marsh, 1869**

**Holotype** YPM 516.

**Horizon** Lower Cretaceous (Barremian) Ilhas Formation, Bahia series ("arenaceous shale").

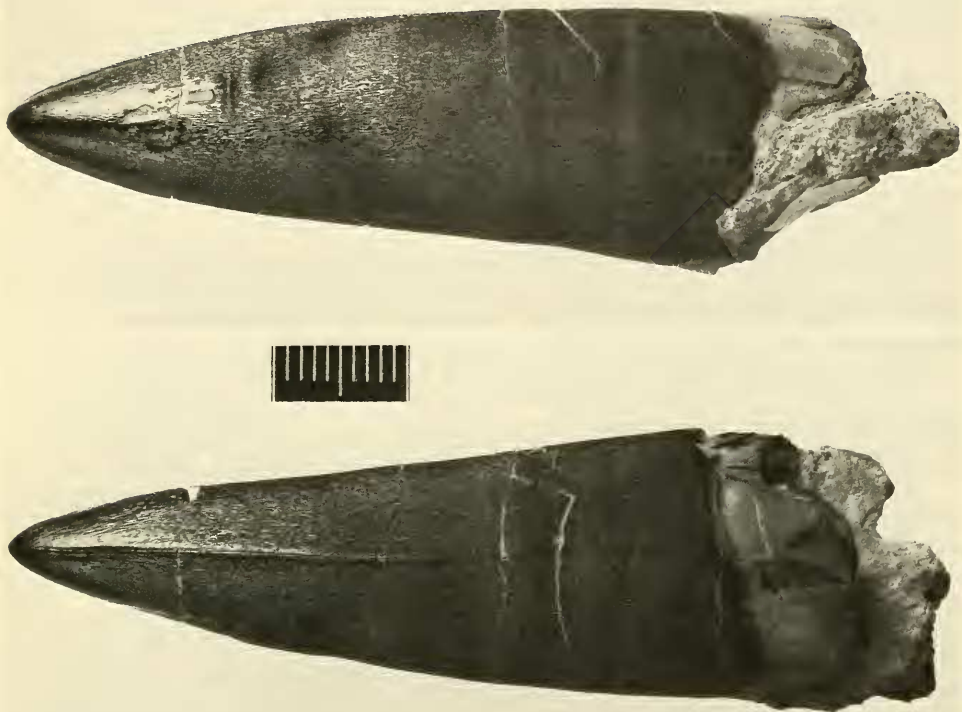
**Locality** Near Plantaforma Station, on the Bahia and San Francisco Railway, approximately 10 km north of Bahia, Recôncavo (Bahia) Basin, northeast coast of Brazil.

**Collector** C. F. Hart, 1867.

**Material** A single isolated tooth lacking root (Fig. 4).

**Remarks** This tooth, described by Marsh (1869) without illustration, is very large (57 × 21 mm) and robust with a somewhat unusual appearance. A prominent carina occurs along the anterior and posterior sides of the tooth; the lateral surfaces are textured with very fine, crenulated striae, a supposedly diagnostic characteristic. Similar teeth were figured by Allport (1860) from the same freshwater sediments at nearby Fort Monseratte (approximately 6 km southwest of Plantaforma). Another tooth of this type is present in a massive, elongate, terminally expanded mandibular symphysis from the same horizon, near Setubal, Brazil (approximately 10 km north of Plantaforma) (Mawson and Woodward 1907). This mandible and associated skull fragments, a large dorsal



**Fig. 4**

*Right*) *Sarcosuchus hartti*, holotype, YPM 516, lateral aspect, scale in millimeters; *left*) same specimen, ?anterior aspect.

osteoscutae, and amphicoelus vertebrae are presumed to represent the same taxon as Marsh's (1869) isolated tooth.

The accessory material from Setubal, particularly the broad, rectangular osteoscutae with its pronounced anterior articulatory peg are 'goniopholid' in character and were assigned to *Goniopholis hartti* by Mawson and Woodward (1907). However, this feature is not unique to *Goniopholis* Owen 1841 (1842) and the assignment to *Goniopholis* is not justified.

The fossils are in no way referable to *Crocodylus* ('*Crocodylus*'). Buffetaut and Taquet (1977), in reviewing the Setubal material, have shown that it is attributable to *Sarcosuchus* de Broin and Taquet 1966, a giant longirostrine form with pholidosaurid affinities. We accept their conclusion that the Yale specimen, although a single tooth, is referable to this taxon on the basis of a shared morphology and should be known as *Sarcosuchus hartti* (Marsh 1869).

***Crocodylus herpichanus* Troxell, 1925a**  
[See *Crocodylus grinnelli herpichanus*  
Troxell, 1925a]

***Crocodylus liodon* Marsh, 1871a**

**Holotype** YPM 1350(b).

**Accession Number** 131.

**Catalogue Entry Date** 1923.

**Horizon** Eocene (Lutetian, Bridgerian),  
Bridger Formation, probably Bridger B of  
Matthew (1909) (upper Black's Fork Member).

**Locality** Grizzly Buttes, near Fort Bridger,  
probably in Sec. 28, T14N, R115W, Bridger  
Basin, Uinta County, Wyoming.

**Collector** C. T. Ballard, Yale College  
Scientific Expedition, 1870.

**Material** A very fragmentary skeleton  
including several vertebrae, the left quadrate,  
rostral fragments, and articulares and  
surangulars.

**Remarks** '*Crocodylus*' *liodon* shares with the  
type specimen of *C. affinis* a divided  
retroarticular fossa with a depressed lateral  
lip, a surangular that forms the anterolateral  
part of the articular fossa, a short and narrow  
medial surface of the divided articular fossa,  
and a large dorsal surface of the  
quadratojugal extending lateral to the  
quadrate's articular condyle. We find no basis  
for recognizing '*C.*' *liodon* as a distinct taxon,  
and therefore consider it a junior synonym of  
*C. affinis*.

***Crocodylus vorax* Troxell, 1925a**

**Holotype** YPM 249.

**Accession Number** 755, box 7.

**Catalogue Entry Date** 16 September 1926.

**Horizon** Eocene (Lutetian, Bridgerian)  
Bridger Formation ("Greensand formation"),  
probably Bridger A of Matthew (1909) (lower  
Black's Fork Member).

**Locality** Near Red Dog Buttes, Bridger  
Basin, Wyoming.

**Collector** J. Heisey, 11 June 1875.

**Material** A crushed, partial skull and  
mandible in association with mammalian  
vertebrae (possibly of *Hyrachyus*); various  
limb elements.

**Remarks** The type skull was accurately  
figured both by Troxell (1925a) in his  
description of '*Crocodylus*' *vorax* and by  
Langston (1975). It is clear from the  
carnosaur-like (ziphodont) dentition and the  
laterally compressed nature of the skull that  
this is a valid species distinct from other  
Bridger crocodyles. It is not referable to  
*Crocodylus*. Although *Limnosaurus ziphodon*  
(Marsh 1871a) is most probably identical,  
typological problems limit the availability of  
this name. Therefore, Langston (1975) has  
placed this species within the genus  
*Pristichampsus* Gervais 1853, a proposal  
accepted here.

**Diagnosis** *Pristichampsus vorax* (Troxell,  
1925a). Larger than *Pristichampsus rollinoti*  
(Gray 1831), with slightly wider and shorter  
snout, and a greater number of teeth in the  
maxilla (16 vs. 13) (Langston 1975).

***Crocodylus ziphodon* Marsh, 1871a** [See  
*Limnosaurus ziphodon* (Marsh, 1871a)].

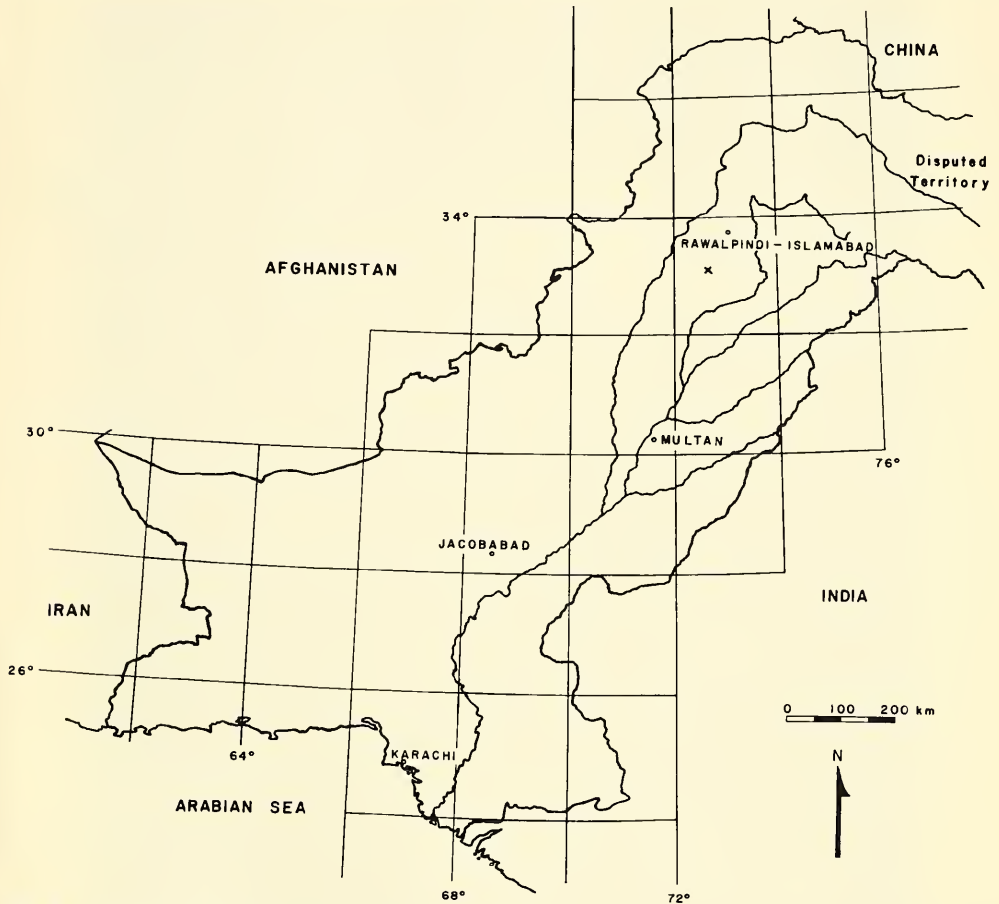
***Diplosaurus felix* Marsh, 1877**

**Holotype** YPM 517.

**Accession Number** 986.

**Catalogue Entry Date** 31 January 1910.

**Horizon** Upper Jurassic (Kimmeridgian)

**Fig. 5**

Map of Pakistan showing approximate locality of  
*Gavialis lewisi*, YPM 3226, as indicated by cross.

Morrison Formation, clay pebble  
conglomerate.

**Locality** Morrison, Colorado.

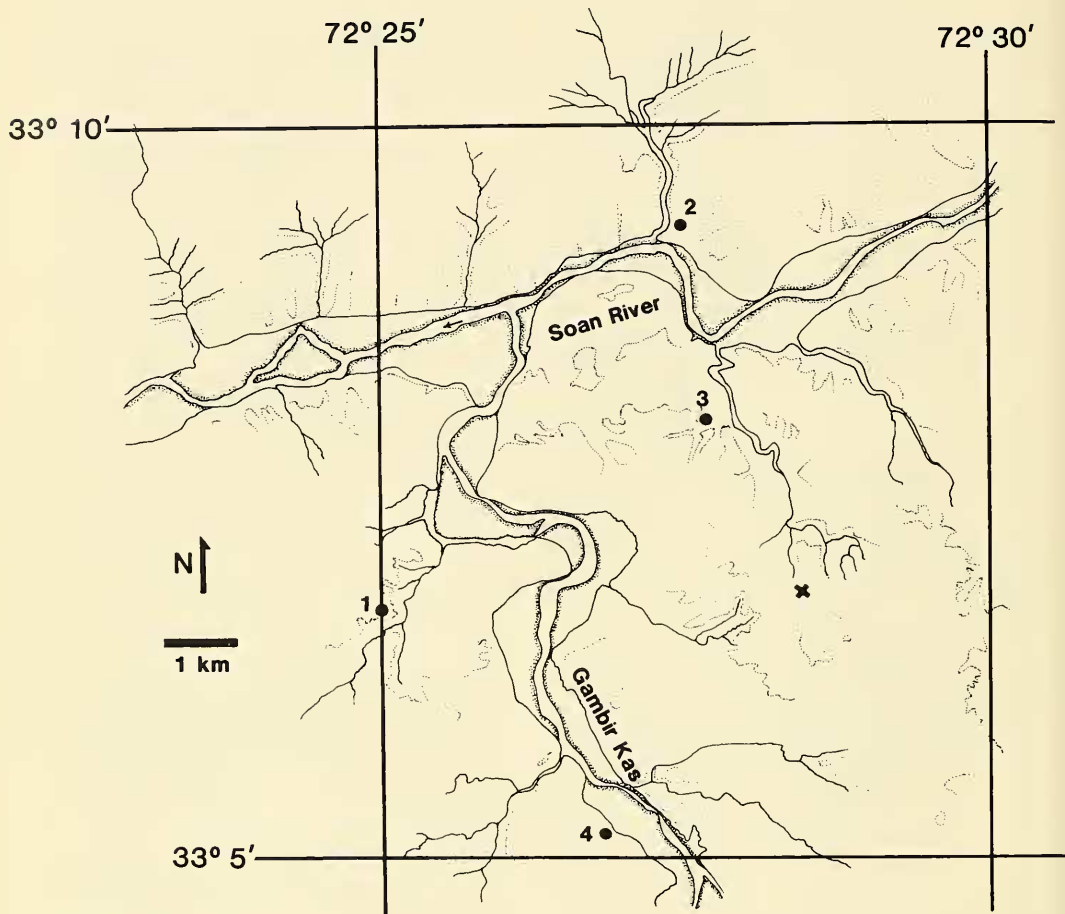
**Collector** B. F. Mudge, A. Lakes, and H. C.  
Beckwith, 1877.

**Material** The dorsal portion of the skull and  
associated postcranial fragments, including a  
partial humerus.

**Remarks** The taxon was described by  
Marsh (1877) on the basis of the skull roof's  
ventral aspect. This surface, exposed only as

the heavily weathered ventral surface of the  
dorsal dermal roofing bones, provided little in  
the way of diagnostic information. Recent  
preparation of the material has exposed the  
dorsal surface of the skull and a more  
complete description of the material is being  
undertaken by Langston (personal  
communication, 1988).

As with many specimens collected before  
the 20th century, detailed anatomical analysis  
and comparison with other taxa was lacking  
from the original description of this fossil.  
Marsh's (1896, 1897) figure was largely  
inferential as it depicted the cranial roof which  
was not exposed until very recently. The



**Fig. 6**  
Detailed locality area of *Gavialis lewisi*, YPM 3226.  
Locality indicated by cross. Numbers 1, 2, 3, and 4  
represent the villages of Naragghi, Kot Maliaran,  
Mathrala, and Marjan, respectively. Dhok Pathan lies  
along the north bank of the Soan, just west of the  
limits of this map.

specimen clearly has goniopholid affinities, in sharing with *Goniopholis* a very distinctly shaped premaxillary area. The long thin snout and large external nares with no nasal participation are also distinctive.

*Diplosaurus felix* has frequently been synonymized with *Goniopholis*. Langston (personal communication, 1987) suggests also the possibility of synonymy with the distinct goniopholid taxon *Eutretraunosuchus* Mook 1967. Awaiting detailed redescription of this

specimen (Langston, in preparation) complete rediagnosis of this specimen is premature. Nevertheless, *Diplosaurus felix* apparently represents a distinct species of medium-sized mesoeucrocodyle (sensu Clark 1986).

***Diplosaurus nanus* Marsh, 1895a**

**Holotype** YPM 518.

**Fig. 7**

Top) *Gavialis lewisi*, holotype, YPM 3226, dorsal aspect, scale in centimeters; bottom) same specimen, ventral aspect.

**Fig. 8**

*Gavialis lewisi*, holotype, YPM 3226, occipital aspect.

**Catalogue Entry Date** 31 January 1910.

**Horizon** Middle or Upper Jurassic, Sundance Formation or equivalent ("Baptanodon beds").

**Locality** Canyon at Sheep Creek (Sage Creek Cañon?), Green River Valley, Utah.

**Collector** O. C. Marsh, 8 October 1870.

**Material** A single, poorly preserved right humerus.

**Remarks** In spite of Marsh's (1895a) confidence in assigning this specimen to a new species, it is unquestionably a nondiagnostic fossil. *Diplosaurus nanus* should be regarded as a nomen dubium because of the inadequacy of the type.

***Gavialis lewisi* Lull, 1944**

**Holotype** YPM 3226.

**Accession Number** 4555.

**Catalogue Entry Date** 16 January 1945.

**Horizon** Upper Pliocene Dhok Pathan Formation, Middle Siwalik series.

**Locality** South of Soan (Sohan) River, east of the Gambir Kas, approximately 12 km southeast of Dhok Pathan village, Punjab (now Rawalpindi Province), northeast border of Pakistan, approximately 33°7' N, 72°28' E (Lull's stated latitude of 32°2' N (1944) does not agree with the placement of the specimen locality on Lewis' field map #43) (Figs. 5, 6).

**Collector** G. E. Lewis, Yale North India Expedition, 24 April 1932.

**Field Number** 19.

**Material** A well-preserved skull lacking the rostrum; posterior mandibular fragments (Figs. 7, 8).

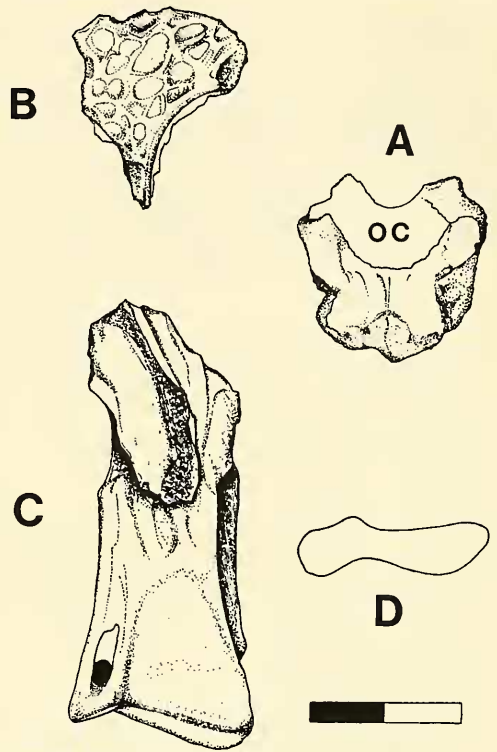
**Remarks** *Gavialis lewisi* was described and

figured by Lull (1944). His description and illustration of the species are fairly accurate, but our reanalysis indicates some ambiguities. For instance, Lull's Figure 1 (p. 419) indicates a paired parietal. Examination of the specimen proves, however, that fused parietals are present as in all other eusuchians. The quadratojugal spines are portrayed in Lull (1944) as small bumps; these are actually the broken bases of apparently once large spines. The position of the frontoparietal suture and other sutures on the parietal table are obscure and cannot be accurately traced, nor can sutures within the supratemporal fenestrae. Likewise, most of the palatal sutures portrayed in Lull's (1944) Figure 2 (p. 420) are indiscernible on the specimen. Posteriorly, the basioccipital tubera are not as bulbous nor directed ventrally as shown by Lull. Rather, they are oriented ventrolaterally and are like those of juvenile *Gavialis gangeticus* (Gmelin 1788).

Due to recent interest in gavialid systematics (Buffetaut 1978a; Hecht and Malone 1972), a review of some of the morphologic features distinguishing *G. lewisi* from *G. gangeticus* is in order. Lull (1944) provided a series of comparisons of *G. lewisi* with other gavialids, while Langston (1965) and Buffetaut (1978a) both considered *G. lewisi* to be very closely related to the extant *G. gangeticus*. Our reanalysis of this specimen indicates that *G. lewisi* is only just distinct as a separate species. The lesser development of the basioccipital tubera, the relatively deeper skull, the smaller supratemporal fenestrae, the presence of labia choanali, and the less drastic transition between snout and braincase primarily differentiate *G. lewisi* from the living species.

**Diagnosis** *Gavialis lewisi* Lull, 1944.

Advanced gavialid sharing with *G. gangeticus* the derived gavialid features of large, circular orbits with everted borders, maxillae lacking interdental pits, large supratemporal fenestrae, longirostrine skull, homodont dentition, basioccipital tubera, and pterygoid bullae; differs from *G. gangeticus* in possessing labia choanali, a deeper skull, relatively smaller supratemporal fenestrae and basioccipital



**Fig. 9**

A, *Thecachampsoides minor*, holotype, YPM 282, basioccipital, occipital aspect, oc—occipital condyle, scale in centimeters; B, same specimen, fused parietals, dorsal aspect, anterior to bottom; C, same specimen, right quadrate, dorsal aspect, lateral surface to right; D, same specimen, right quadrate, articular aspect, dorsal surface on top.

tubera, large postorbital exposure on the skull's dorsal surface, and a mediadorsal quadrate ridge (modified from Langston 1965 and Lull 1944).

### *Gavialis minor* Marsh, 1870

**Holotype** YPM 282.

**Catalogue Entry Date** 16 September 1926.

**Horizon** Eocene (Ypresian) Manasquan Formation ("Greensand").

**Locality** Shark River, Monmouth County, New Jersey.

**Collector** Hugh Hurley, 1870.

**Material** The fragmentary remains of a skull, including portions of both quadrates, the incomplete parietal, basioccipital/basisphenoid, right postorbital, and right angular; four cervical vertebrae, four partial anterior dorsal vertebrae, one thoracic vertebra, and the biconvex first caudal vertebra (Fig. 9).

**Remarks** This taxon is based upon an incomplete skeleton that was never figured. In the original description, Marsh (1870) suggested that the skull was of the "gavial type" and represented an adult of the species. In reality, the remains are too scanty for such a determination; however, the narrow anterior parietal process does suggest that large supratemporal fenestrae (seen in many longirostrine forms) were present, and the extensive ossification of the braincase and vertebrae are characteristic of adult eusuchians. Not discussed in the original description were the primitive eusuchian type of basioccipital/basisphenoid complex—lacking the derived alligatorid features of a deep and laterally constricted braincase floor and a ventrally elongate occipital surface (the latter typical of caimans), and the gavial-like feature [also present in many other fossil longirostrine crocodylomorphs (*sensu* Norell, in press)] of expanded basal tubera (see, e.g., Hecht and Malone 1972).

The quadrates are short and relatively straight; their articular surfaces are hourglass shaped with inflected medial processes. These conditions are present in several members of the Crocodylia but are not seen in the extant gavial. Marsh (1870) indicated that a characteristic feature of the quadrate of this specimen was the large siphonial foramen present on its medial surface. Actually, this foramen has been enlarged by postmortem breakage. The distal end of the left quadrate exhibits a siphonial foramen that is better preserved than that of the right and, while large, is still within the range of variation seen in extant eusuchians.

The parietal is heavily sculptured and

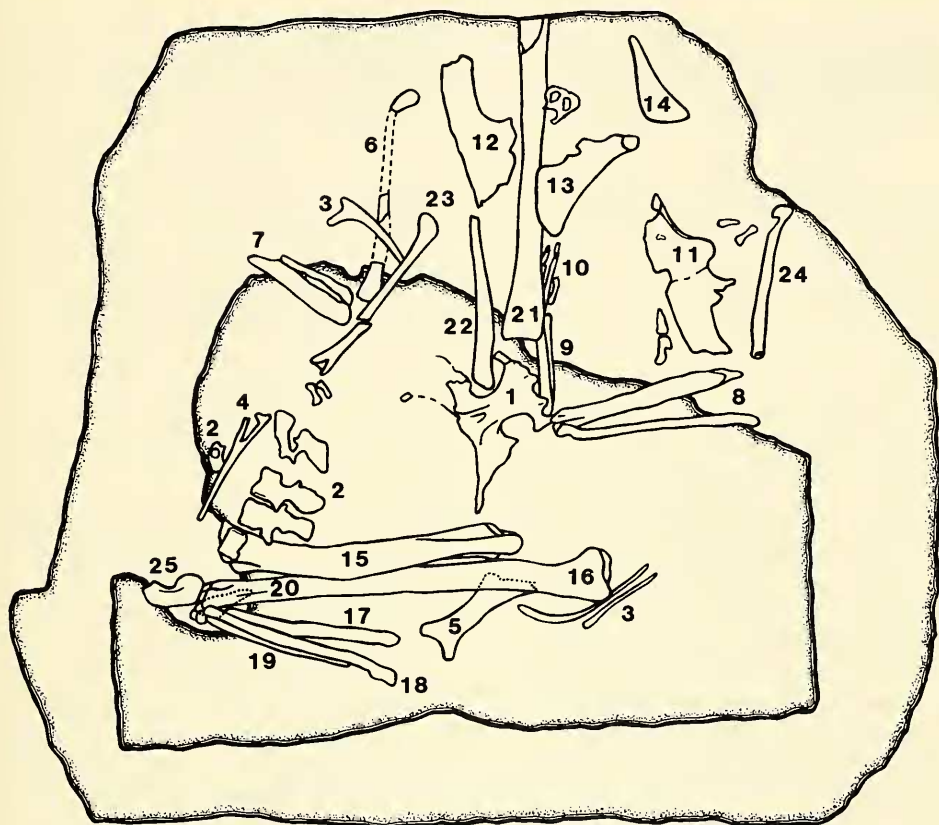
nonpneumatic. Its form indicates that the supraoccipital was excluded from the skull roof, and small ventral depressions just anterior to its posterior margin suggest that it overhung the occipital wall slightly. A large postorbital foramen, similar to that of alligatorids (as well as juvenile crocodylians in general) is present just above the postorbital bar process.

Marsh (1870) believed that the vertebrae of this specimen were peculiar in having transversely ovoid centra; however, this feature is present in many extant eusuchians, especially alligatorids, and in several fossil taxa (see, e.g., Troxell 1925a, fig. 8). The vertebrae are unremarkable and in being procoelous are typical of eusuchian grade crocodylians. Complete fusion and obliteration of sutures between the neural arch and centrum confirm Marsh's (1870) suspicion that the individual was adult.

In assessing the affinities of *Gavialis minor*, Marsh (1870) suggested that it might prove to be generically identical with the much larger *Thecachampsa squankensis* Marsh 1869, also from the Eocene of New Jersey. Sadly, Marsh (1869, 1870) merely noted the existence of material that he ascribed to a new species, *T. squankensis* (under the generic misspelling *Thecochampsa*). He never described the material nor designated a type specimen. It is now impossible to identify this material in the Yale collections. The genus *Thecachampsa* Cope 1867, based on nondiagnostic, isolated teeth from the Miocene of Charles County, Maryland, was itself regarded by Marsh (1870) as unrecognizable, thus YPM 282 was provisionally placed by him in the genus *Gavialis* Oppel 1811.

It is tempting to consider *G. minor* a nomen dubium on the basis of problematic material; however, an adequate diagnosis for the taxon can be presented. We believe that the fossil represents a unique crocodylian worthy of generic distinction although its relationships are difficult to determine without a better but as yet uncompleted phylogenetic depiction of Early Tertiary eusuchians. Obviously, the name *Gavialis* cannot be retained for this specimen, as it possesses not a single unmistakable



**Fig. 10**

Schematic diagram of *Hallopus victor*, holotype, YPM 1914, combining part and counterpart blocks and illustrating relative positions of bones. 1, sacrum; 2, caudal vertebrae; 3, ribs; 4, chevron; 5, scapula; 6, right humerus; 7, right radius and ulna; 8, left radius and ulna; 9, left radiale and ulnare; 10, left manus; 11, 12, ilia; 13, 14, ischia; 15, left femur; 16, left tibia; 17, left metatarsal II; 18, left metatarsal III; 19, left metatarsal IV; 20, left metatarsal V; 21, right tibia; 22, right fibula; 23, left metatarsal?; 24, pubis?; 25, left calcaneum.

gavial feature. We have chosen to consider the specimen a new, distinct taxon with eusuchian affinities on the basis of its procoelous vertebrae and a recessed postorbital bar. It differs from the Cretaceous

eusuchian *Thoracosaurus* Leidy 1852, most notably on the basis of its much narrower interfenestral (parietal) bar. Steel (1973) suggested that this species had crocodyline affinities merely on the basis of Marsh's (1870)

comparison with *T. squankensis*. Our examination, however, finds no evidence for preferential relationship with any eusuchian group at this time.

### ***Thecachampsoides*, new genus**

**Etymology** *Thecachampsa* + *oides* (Latin "like") after earlier comparisons to *Thecachampsa*.

**Type Species** *Gavialis minor* Marsh, 1870.

**Diagnosis** *Thecachampsoides minor* (Marsh, 1870), new combination.

Eusuchian crocodylian distinguished by the unique suite of features of small adult size, large supratemporal fenestrae as in *Thoracosaurus*, narrow parietal bar, relatively large siphonial foramen of the quadrate, basisphenoid lacking basal tubera, floor of braincase shallow and laterally constricted, occipital wall concave, parietal lacking pneumatization, vertebrae procoelous, centra of thoracic vertebrae transversely ovoid. This combination of characters is not found in any other known longirostrine eusuchian.

***Goniopholis felix* (Marsh, 1877)** [See *Diplosaurus felix* Marsh, 1877]

***Goniopholis hartti* (Marsh, 1869)** [See *Crocodylus hartti* Marsh, 1869]

***Hallopus victor* (Marsh, 1877)**

**Holotype** YPM 1914.

**Accession Number** 958.

**Catalogue Entry Date** 10 March 1908.

**Horizon** Probably Middle Jurassic (Callovian), lower Ralston Creek Formation.

**Locality** In float on west side of Oil (Four

Mile) Creek, probably below "The Nipple," Garden Park, approximately 5 km north of Cañon City, Fremont County, Colorado (T17S, R70W).

**Collectors** J. Jennings, S. C. Robinson, for D. Baldwin, April 1877.

**Material** Associated, partially articulated skeletal elements contained within part and counterpart matrix blocks: sacrum, pelvis, scapula, incomplete fore and hind limbs, a few fragmentary vertebrae, ribs, and chevrons. A composite diagram of the specimen is provided in Figure 10.

**Remarks** *Hallopus victor*, known only from the type specimen, has been the object of controversy for over 100 years. Originally "described" (Marsh 1877) as a distinct species of the ornithomimid dinosaur *Nanosaurus*, this fossil was later (Marsh 1881) transferred to the newly created genus *Hallopus* upon the realization of its unique character, particularly with regard to its large calcaneal tuber. It was, nevertheless, generally considered by Marsh as dinosaurian (although only questionably so in Marsh 1882, 1890), usually as a theropod. The first adequate description of the specimen (Marsh 1890) included a figure of the left hindlimb with its pronounced heel as preserved. This was later supplanted with reconstructions of the fore and hind limbs (Marsh 1895b). Von Huene and Lull (1908) suggested that the animal was not a dinosaur, but rather allied with the Thecodontia, while von Huene (1914) and many subsequent workers classified *Hallopus* as a coelurosaur. The descriptions provided by von Huene and Lull (1908), and especially von Huene (1914), are more detailed than those of Marsh (1877, 1881, 1890) and include additional figures, notably photographs of the matrix blocks (von Huene 1914), yet the identifications of individual bones provided by Marsh (1877, 1881, 1890) now generally appear the more accurate.

The best and most detailed study of *Hallopus* to date was supplied by Walker (1970). In it he confirmed Marsh's (1890)

interpretations of the ischium and sacrum while correcting previous misidentifications of radius, ulna, radiale and ulnare. Based upon this work, Walker (1970) concluded that *Hallopus* was neither a dinosaur nor a thecodont, but a small, gracile, semiterrestrial crocodylomorph akin to *Pedeticosaurus* Van Hoepen 1915, and *Sphenosuchus* Haughton 1915, and belonging to the suborder Paracrocodylia Walker 1968. Walker (1970) retained the taxon Hallopoda Marsh 1881 as an infraorder.

Whether or not Walker's (1968, 1970) taxonomy is accepted, it is clear that *Hallopus* represents a derived, cursorial crocodylian (crocodylomorph). The best evidence for this assignment is the crurotarsal ankle joint with a greatly lengthened calcaneal tuber. This form of tarsus excludes *Hallopus* from the dinosaurs, all of which exhibit an advanced mesotarsal condition. Other than in crocodylians, the fully developed crocodyloid-normal configuration of the *Hallopus* tarsus, with the articular peg of the joint on the astragalus and the socket in the calcaneum, is found only in rauisuchids and in the aberrant aëtosauroids. All thecodont affinities can be ruled out, however, by the open acetabulum evident in the ilium of *Hallopus*.

Other crocodylian characteristics observable in the present fossil are the elongate proximal carpals, broad sacrum comprising two vertebrae with stout sacral ribs, the flat bladellike ischium (very similar to that of *Protosuchus* Brown 1934), and a metatarsus consisting of lengthy metatarsals I-IV, with a much reduced, clawlike metatarsal V. *Hallopus* resembles pedeticosaurid crocodylomorphs in its long, gracile, hollow-boned limbs, and is particularly noteworthy for its extremely elongate calcaneum, radiale, and ulnare.

The element identified by Walker (1970) as the pubis is very poorly preserved and is actually indeterminate. It more likely represents the impression of the second ischium. Walker (1972) suggested a second candidate for the pubis but this, while more likely, is also questionable. It is a long, thin, rodlike bone with an apparent articular facet

and possible obturator notch (seemingly not an artifact) at one end. The opposite end is incomplete. The orientation of the "pubis" is a separate question, however, and the posteriorly rotated position suggested by Walker (1972) is entirely conjectural. Such a reconstruction was evidently influenced by his desire (since abandoned) to place the origin of birds within the Crocodylomorpha.

A second controversy surrounding this specimen involves the question of its stratigraphic provenance and the age of the "*Hallopus* beds." Marsh (1891) asserted that these beds lay below his "*Atlantosaurus* beds" (i.e., Morrison Formation) and were distinct from them. Because of the incomplete state of stratigraphic knowledge of the western interior at the time, Marsh's (1877, 1881, 1891) estimates of the age of the "*Hallopus* beds" ranged from uppermost Jurassic to Triassic. Williston (1905), having visited the exact locality, maintained that the fossil block had fallen from an escarpment of red sandstone which he believed to be Triassic. This interpretation stood unchallenged until Schuchert (1939), largely on the basis of correspondence between Marsh and Baldwin, placed the *Hallopus* horizon near the top of the Morrison Formation, a conclusion accepted by Walker (1970).

In fact, contrary to Schuchert (1939), red beds of the type composing the *Hallopus* matrix are unknown from the Morrison at Garden Park or elsewhere. This matrix is not a chocolate brown nodule as insisted upon by Schuchert (1939), but clearly a resistant, mature, red silt with intermittent clasts of red mudstone and a silica cement. Similarly, the oxidized, bone-white nature of the fossil's preservation is unknown in the Morrison Formation. Nevertheless, it is now also known that Triassic sediments are not present in the Garden Park area, but rather the extensive red beds there are primarily of Pennsylvanian and Permian age. However, at the *Hallopus* locality of Oil Creek Canyon, restricted terrestrial sediments of the Middle Jurassic (Callovian) lower Ralston Creek Formation occur below the Morrison Formation (Berman

et al. 1980; Fredrickson et al. 1956). More typical gypsiferous marine shales of the upper Ralston Creek Formation occur to the north and east. However, at Garden Park the Ralston Creek sediments consist of red and green siltstones (Mitchell 1957) and most likely represent the source of the *Hallopus* float block.

**Diagnosis** *Hallopus victor* (Marsh, 1877).

*Scapula blade narrow; limb-bones hollow; proximal carpals greatly elongated, in contact throughout their length, proximal carpal joint apparently immobile but distally a roller-joint with the metacarpus, probably no other carpals; metacarpals I and III wedging out proximally, manus small, compressed; iliac blade long and high, curving down behind; femur with 'pseudointernal' trochanter and lesser trochanter, fourth trochanter an inconspicuous narrow ridge, head offset, subspherical; tibia and fibula very slender, longer than femur; tarsus greatly compressed, dorso-lateral process of astragalus visible in lateral view, distal end of fibula posterior to astragalus, calcaneum very narrow, with long tuber; lateral distal tarsal large; pes functionally tridactyl, metatarsals II–IV elongated, firmly fixed together proximally, metatarsal I a long slender splint recessed into metatarsal II, metatarsal V reduced, pointed. (Walker 1970).*

***Hyposaurus ferox* Marsh, 1871b**

**Holotype** YPM 2794.

**Catalogue Entry Date** 9 July 1937.

**Horizon** Uppermost Cretaceous (Maastrichtian) Hornerstown Formation, "middle marl bed" ("Greensand").

**Locality** Birmingham, New Jersey.

**Material** Two isolated teeth.

**Remarks** Marsh (1871b) presented no figures of these teeth to accompany his assignment of the material to a new species. However, the descriptions of the teeth, particularly that noting one as being long, pointed, strongly ribbed, and bearing a sharp posterior carina, are consistent with the notion that they represent teeth of *Hyposaurus* Owen 1849 (although teeth of such other taxa as *Thoracosaurus*, known from the same deposits, are similar). In any event, it is highly unlikely that a separate species can be diagnosed on the basis of these teeth and we consider this taxon a nomen dubium. Compounding the problem, the material has apparently been lost; a thorough search of the collection failed to produce it.

***Hyposaurus natator* Troxell, 1925b**

**Holotype** YPM 985.

**Accession Number** 83.

**Catalogue Entry Date** 16 September 1926.

**Horizon** Uppermost Cretaceous (Maastrichtian), Hornerstown Formation, "middle marl bed" ("Greensand").

**Locality** Cream Ridge Marl Company pit, Hornerstown, Monmouth County, New Jersey.

**Collector** J. G. Meirs.

**Material** Partial cranium and mandibles, largely complete postcranial skeleton.

**Remarks** *Hyposaurus natator* was accurately described by Troxell (1925b). Recent analyses have satisfactorily indicated that *Hyposaurus* is a dyrosaurid crocodylian (Buffetaut 1976, 1980), not a goniopholid. In fact, *Hyposaurus natator* is so similar to many Cretaceous and early Tertiary dyrosaurids that little support can be found for its uniqueness. *Hyposaurus natator* shares with North African forms even such subtle features as an anterior spine on the postorbital (see Buffetaut 1978b,

1980). Postcranially, all dyrosaurids exhibit little intertaxonal variation (Moody and Buffetaut 1981; Storrs 1986).

Troxell (1925b) designated YPM 380, an incomplete mandible and fragmentary postcrania, as part of the type material ("heautotype"). YPM 380 represents a second individual from the type locality. It shares the typical dyrosaurid feature of a long thin mandible formed of fused dentaries and splenials that is tubular in shape with procumbent anterior teeth. YPM 380 differs from the North African material described by Buffetaut (1978b, 1980) and the Swedish material of Thevinin (1911) in having deeper interdental pits. This is a feature also found in *Rhabdognathus* Swinton 1930. The relevant area is not preserved in YPM 985. YPM 380 resembles other dyrosaurids in possessing a large pit just anterior to the seventh dentary tooth. Dyrosaurid crocodylians are in need of complete revision, as much of the new material is yet to be described in detail while much of the older material requires redescription. Langston (in press) discusses *Rhabdognathus* in detail and deals with part of the dyrosaurid problem. Awaiting this work, however, we provisionally retain *H. natator* as a distinct species. It should not at this time be specifically equated with *Hyposaurus rogersii* Owen 1849. *H. rogersii*, the type species of the genus, is itself questionably diagnostic, consisting only of a cervical vertebral centrum and an anterior dorsal centrum.

The Cream Ridge–Hornerstown region is a classic fossil locality, having produced many specimens for Marsh, Cope, and Leidy, including numerous types. A marine unit, the Hornerstown Formation is composed almost exclusively of glauconitic sand and probably represents a period of slow, outer shelf deposition. A deep water, low oxygen setting with little terrigenous input has been proposed for the Hornerstown paleoenvironment (Gallagher et al. 1986).

**Diagnosis** *Hyposaurus natator* Troxell, 1925b.

*rostrum, orbits lateral, supratemporal foramen elongated; teeth ridged longitudinally, compressed, pointed, directed outward and forward in the mandible; quadrate strongly bent downward, its condyle undivided by a groove; the vertebral hypapophyses characteristically strong, anterior cervicals narrow, those more distant robust and rounded on the ends [amphiplatyan] vertebral centra unequal in length at top and bottom; neural spines of anterior dorsals of great height, centra of posterior dorsals and lumbers rounded and simple in form, caudals laterally compressed having short ribs; acetabulum deep, femoral articulation posterior rather than ventral in position, "pubic" bone enormously elongated, ischium heavy proximally but with slender, pointed blade, femur-head curved beak-like forward; scapula-blade extended to the fore, its coracoid articulation narrow, coracoid shaft and blade slender and small, deltoid crest of humerus weak.* (Troxell 1925b).

***Hyposaurus natator oweni* Troxell, 1925b**

**Holotype** YPM 753.

**Accession Number** 77.

**Catalogue Entry Date** 21 April 1950.

**Horizon** Uppermost Cretaceous (Maastriechian), Hornerstown Formation, "middle marl bed" ("Greensand").

**Locality** West Jersey Marl Company pit, Barnsboro, New Jersey.

**Collector** J. C. Voorhies, 14 January 1870.

**Material** Partial skeleton and fragmentary skull. Also included in the type material is an anterior lower jaw fragment of a second individual.

**Remarks** Troxell (1925b) described

*Skull long and converging uniformly to the*

*Hyposaurus natator oweni* as a subspecies of *Hyposaurus natator* Troxell 1925b.

Unfortunately, on page 506 of this work, Troxell refers to YPM 753 as *Hyposaurus oweni*. This specimen is larger (approximately 2×) than the type of *H. natator* (YPM 985) but shows few characters which may distinguish it. The features of the pelvis discussed by Troxell (1925b) are so poorly preserved that they are of little value. The fused splenials associated with YPM 753 actually belong to another individual. Their small size, slightly larger than those of YPM 985, indicates that they could not have belonged to the present specimen (YPM 753).

The type material of *H. natator oweni* probably represents a composite of individuals. We view the taxon as undiagnosable. The material is dyrosaurid but its extremely fragmentary nature makes its assignment to any species difficult. Most of it probably pertains to *Hyposaurus natator* Troxell 1925b.

***Hyposaurus oweni* Troxell, 1925b** [See ***Hyposaurus natator oweni* Troxell, 1925b**]

***Limnosaurus ziphodon* (Marsh, 1871a)**

**Holotype** (?) YPM 1347 and YPM 5890 (possibly also YPM 1348).

**Accession Number** (?) 136 or 249+.

**Catalogue Entry Date** 25 January 1910 (possibly also 16 September 1926).

**Horizon** Eocene (Lutetian, Bridgerian), Bridger Formation, probably Bridger B of Matthew (1909) (upper Black's Fork Member).

**Locality** Grizzly Buttes, near Fort Bridger, probably in Sec. 28, T14N, R115, Bridger Basin, Uinta County, Wyoming.

**Collectors** O. C. Marsh, J. R. Nicholson, and H. B. Sargent, 1870.

**Material** Specified (Marsh 1871a) only as

including ziphodont teeth, a quadrate and other parts of the skull, and dorsal osteoscutes.

**Remarks** Langston (1975) has fully discussed the typological problems associated with this taxon and its possible type material. In summary, the description of '*Crocodylus*' *ziphodon* as a new species by Marsh (1871a) did not include a registry number nor an illustration of the holotype. Similarly, when Marsh (1872) proposed the generic name *Limnosaurus* for this species after examining "additional remains . . . , since obtained," no information allowing identification of the hypodigm was forthcoming. Troxell (1925a) identified a portion of this material as the extremely fragmentary YPM 1347, but Langston (1975) is correct in asserting that YPM 1347 comprises more than one individual and taxon. Additionally, this material bears the accession number 249+ which conflicts with the presumed date of collection and the expected accession number of 136. Adding to the confusion are several teeth and a scute, associated with YPM 1347, unnumbered, or bearing YPM 1348, which may form part of the type assemblage, whereas the distal end of a right quadrate, part of YPM 1347, has been renumbered as YPM 5890.

If the holotype of *Limnosaurus ziphodon* is included in this material it cannot be certainly recognized and both '*C.*' *ziphodon* Marsh 1871a and *Limnosaurus* Marsh 1872 must be regarded as *nomina nuda* (Langston 1975). However, the quadrate numbered as YPM 5890 and each of the noted ziphodont teeth are characteristic of, and undoubtedly pertain to, *Pristichampsus vorax* (Troxell 1925a). Because of the preceding difficulties *Pristichampsus vorax* (Troxell 1925a) is the only name available for North American ziphodont crocodyles.

***Macelognathus vagans* Marsh, 1884**

**Holotype** YPM 1415.

**Accession Number** 1394.



**Fig. 11**  
 Left quadrates of *Thoracosaurus*. Dorsal surfaces to left, not to scale. A, *Thoracosaurus meirsanus*, holotype, YPM 404; B, *Thoracosaurus mullicensis*, holotype, YPM 283.

**Catalogue Entry Date** 24 April 1909.

**Horizon** Upper Jurassic (Kimmeridgian), Morrison Formation.

**Locality** Quarry 9, Como Bluff, Albany County, Wyoming (SW ¼ Sec. 12, T22N, R77W).

**Collector** W. H. Reed, 1880.

**Material** Partial dentaries (symphysis and anterior portions of mandibular rami).

**Remarks** A problematic taxon that, when described by Marsh (1884), was made the basis for a new order of reptiles, the Macelognatha. Although Marsh (1884) cryptically suggested that the species was represented by "various remains," only a pair

of dentaries were figured and described, and only these can now be assigned to the type. Ostrom (1971) has redescribed the fossil, referred it to the Crocodylia (traditional usage), and discussed the evidence for its possible association with obviously crocodylian remains. Nevertheless, the fossil differs from known crocodylians in the possession of an unusual, spatulate, edentulous mandibular extremity. This unique specimen is obviously an aberrant form, questionably crocodylian, but neither is it readily referable to any other order.

**Diagnosis** *Macelognathus vagans* Marsh, 1884. Distinguished from all known crocodylians by a spatulate dentary symphysis with an edentulous extremity; symphyseal suture long with splenial participation.

***Nanosaurus victor* Marsh, 1877** [See *Hallopus victor* (Marsh, 1877)].

***Pristichampsus vorax* (Troxell, 1925a)**  
 [See *Crocodylus vorax* Troxell, 1925a and *Limnosaurus ziphodon* (Marsh, 1871a)].

***Sarcosuchus hartti* (Marsh, 1869)** [See *Crocodylus hartti* Marsh, 1869].

***Thecachampsoides minor* (Marsh, 1870)**,  
 new combination  
 [See *Gavialis minor* Marsh, 1870]

***Thoracosaurus meirsanus* Troxell, 1925c**

**Holotype** YPM 404.

**Catalogue Entry Date** 16 September 1926.

**Horizon** Upper Cretaceous ("Greensand"), probably Hornerstown Formation.

**Locality** Cream Ridge Marl Company pit, Hornerstown, Monmouth County, New Jersey.

**Collector** J. G. Meirs.

**Material** Cranial fragments including the skull roof, and extremely fragmentary portions of the postcranial skeleton.

**Remarks** This material, like so many specimens from the New Jersey Greensand, suffers from degenerative pyrite "disease." It has been continuously crumbling since its original description. The most complete elements are the reassembled posterior cranial roofing elements. The poor state of preservation renders the specimen unremarkable, as few details can be studied. Consequently, nothing can be added to the original description.

North American *Thoracosaurus* remains are for the most part extremely fragmentary. Only *T. neocesariensis* (De Kay 1842) is known from adequate material. Carpenter (1983) synonymized *T. meirsanus* and *T. mullicensis* (described below) with *T. neocesariensis*. Though possibly premature, this suggestion is provisionally accepted here; two forms may actually be present.

*T. meirsanus* and *T. mullicensis* exhibit two distinct quadrate morphologies (Troxell 1925c). In YPM 404 (*T. meirsanus*) the quadrate is medially constricted with a laterally oriented articular surface of the medial condyle. Posteriorly, the quadrate is excavated by a large depression. YPM 283, *T. mullicensis*, has a quadrate that is much less hourglass-shaped and lacks a pronounced posterior depression (Fig. 11). Varieties of quadrate shape in crocodylian morphology have been used by several workers (e.g., Langston 1975) in taxonomic studies. The quadrates of *T. neocesariensis* are not preserved, but those of the Swedish *Thoracosaurus scanius* Troedsson 1924 are similar to those of *T. meirsanus*.

We provisionally accept Carpenter's (1983) synonymy of *T. meirsanus* with *T. mullicensis* and *T. neocesariensis*, pending detailed revision of *Thoracosaurus*, but Carpenter's diagnosis is based upon ambiguously derived features and complete revision of the entire thoracosaur group and closely related basal

eusuchians is required before these taxa can be properly discussed.

### ***Thoracosaurus mullicensis* Troxell, 1925c**

**Holotype** YPM 283.

**Accession Number** (?) 47 (this number does not agree with locality information).

**Catalogue Entry Date** 16 September 1926.

**Horizon** Upper Cretaceous, "marl beds," probably Hornerstown Formation.

**Locality** Mullica Hill, New Jersey.

**Collector** O. C. Marsh, 1872.

**Material** Small fragments of skull and postcrania; severely afflicted with pyrite "disease."

**Remarks** Elements of interest preserved include the quadrates (discussed above), a maxillary fragment with three teeth, and several loose teeth. The fluted teeth resemble those illustrated by Troedsson (1924) for *Thoracosaurus* from Sweden. The maxillary teeth display pronounced wear facets. Because the type material is too fragmentary to allow a proper diagnosis, we conditionally accept Carpenter's (1983) suggestion of synonymy with *T. neocesariensis*. *T. mullicensis*, however, lacks many of the important elements that would allow detailed comparison with other specimens.

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### **Summary of Taxonomic Changes**

**Synonymies** *Crocodylus affinis* Marsh, 1871a includes *C. brevicollis* Marsh, 1871a; *C. grinnelli* Marsh, 1871a; *C. herpichanus* Troxell, 1925a; and *C. liodon* Marsh, 1871a.

**New Genus** *Thecachampsoides minor* from *Gavialis minor* Marsh, 1870.

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**Nomina Dubia** *Diplosaurus nanus* Marsh, 1895a; *Hyposaurus ferox* Marsh, 1871b; *Hyposaurus natator oweni* Troxell, 1925b.

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### Literature Cited

- Allport, S.** 1860. On the discovery of some fossil remains near Bahia in South America. *Q. J. Geol. Soc. London* 16:263–68.
- Berman, A. E., D. Poleschook Jr. and T. E. Dimelow.** 1980. Jurassic and Cretaceous systems of Colorado, p. 111–28. *In* H. C. Kent and K. W. Porter (eds.), *Colorado Geology*. Denver, Rocky Mount. Assoc. Geol.
- Bonnaterre, J. P.** 1789. *Tableau Encyclopédique et Méthodique des Trois Regnes de la Nature*. Erpétologie, Paris, Liège.
- Broin, F. de and P. Taquet.** 1966. Découverte d'un crocodylien nouveau dans la Crétacé inférieur du Sahara. *C. R. Acad. Sci. Paris (Sér. D)* 262:2326–29.
- Brown, B.** 1934. A change of names. *Science, n.s.*, 79:80.
- Buffetaut, E.** 1976. Une nouvelle définition de la famille des Dyrosauridae de Stefano, 1903 (Crocodylia, Mesosuchia) et ses conséquences: inclusion des genres *Hyposaurus* et *Sokotusuchus* dans les Dyrosauridae. *Géobios* 9, 3:333–36.
- 1978a. Sur l'histoire phylogénétique et biogéographique des Gavialidae (Crocodylia, Eusuchia). *C.R. Acad. Sci. Paris (Sér. D)* 287, 10:911–14.
- 1978b. Les Dyrosauridae (Crocodylia: Mesosuchia) des phosphates de l'Eocene inférieur de Tunisie: *Dyrosaurus*, *Rhabdognathus*, *Phosphatosaurus*. *Univ. Provence Ann. Geol. Mediterr.* 5, 2:237–56.
- 1980. Les crocodyliens Paleogènes du Tilemsi (Mali): un aperçu systématique. *Palaeovertebrata, Mém. Jubil. R. Lavocat*: 15–35.
- Buffetaut, E. and P. Taquet.** 1977. The giant crocodylian *Sarcosuchus* in the Early Cretaceous of Brazil and Niger. *Palaeontology* 20, 1:203–08.
- Carpenter, K.** 1983. *Thoracosaurus neocesariensis* (De Kay 1842) (Crocodylia: Crocodylidae) from the Late Cretaceous Ripley Formation of Mississippi. *Miss. Geol.* 4, 1:1–10.
- Clark, J. M.** 1986. The relationships of the crocodylomorph archosaurs. Ph.D. dissertation, University of Chicago, unpublished.
- Cope, E. D.** 1867. An addition to the vertebrate fauna of the Miocene period, with a synopsis of the extinct Cetacea of the United States. *Proc. Acad. Nat. Sci. Philadelphia* 1867:138–56.
- 1882. The reptiles of the American Eocene. *Amer. Naturalist* 16:979–93.
- 1884. The Vertebrata of the Tertiary formations of the West. Book I. Report U.S. Geol. Survey Territories 3:1–1009.
- De Kay, J. E.** 1842. *Zoology of New York, or the New York fauna; comprising detailed descriptions of all the animals hitherto observed within the state of New York, with brief notices of those occasionally found near its borders, accompanied by appropriate illustrations. Ill. Reptiles and Amphibia*. Albany.
- Fredrickson, E. A., J. M. DeLay and W. W. Saylor.** 1956. Ralston Formation of Canon City embayment, Colorado. *Bull. Am. Assoc. Pet. Geol.* 40, 9:2120–48.

- Gallagher, W. B., D. C. Parris and E. E. Spamer.** 1986. Paleontology, biostratigraphy, and depositional environments of the Cretaceous—Tertiary transition in the New Jersey Coastal Plain. *The Mosasaur* 3:1–35.
- Gervais, P.** 1853. Observations relatives aux reptiles fossiles de France (première partie). *C.R. Acad. Sci. Paris* 36:374–77.
- Gmelin, J. F.** 1788. *Caroli a Linné Systema Naturae per Regna tria Naturae, secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis.* Editio XIII, aucta, reformata. 1, 3. Gmelin, Lipsia.
- Gray, J. E.** 1831. Synopsis Reptilium or short descriptions of the species of reptiles. Vol. 1, Cataphracta. London, Truettel, Wurtz, & Co. 88 p.
- Houghton, S. H.** 1915. Investigations in South African fossil reptiles and Amphibia. 9. A new thecodont from the Stormberg beds (*Sphenosuchus acutus* g. et sp. nov.). *Ann. S. Afr. Mus.* 12:98–105.
- Hecht, M. K. and B. Malone.** 1972. On the early history of the gavialid crocodylians. *Herpetologica* 28, 3: 281–84.
- Huene, F. R. von.** 1914. Beitrage zur Geschichte der Archosaurier. *Geologische u. Palaeontol. Abh. (N.F.)* 13, 1:1–53.
- Huene, F. R. von and R. S. Lull.** 1908. On the Triassic reptile *Hallopus victor* Marsh. *Am. J. Sci. (Ser. 4)* 25, 146:113–18.
- Langston, W. Jr.** 1965. Fossil crocodylians from Columbia and the Cenozoic history of the Crocodylia in South America. *Univ. Calif. Publ. Geol. Sci* 52:1–169.
- 1975. Ziphodont crocodyles: *Pristichampsus vorax* (Troxell), new combination, from the Eocene of North America. *Fieldiana Geol.* 33, 16:291–314.
- Dyrosaurs (Crocodylia: Mesosuchia) from the Paleocene Umm Himar Formation, Kingdom of Saudi Arabia. *U.S. Geolog. Surv. Bull.*, in press.
- Laurenti, J. N.** 1768. *Specimen medicum, exhibens synopsis Reptilium emendatum cum Experimentis circa Venena et Antidota Reptilium Austriacorum.* Vienna.
- Leidy, J.** 1852. [Descriptions of *Delphinus conradi* and *Thoracosaurus grandis*.] *Proc. Acad. Nat. Sci. Philadelphia* 6:35.
- 1870. [Description of *Crocodylus ellioti*.] *Proc. Acad. Nat. Sci. Philadelphia* 1870:100.
- Lull, R. S.** 1944. Fossil gavials from North India. *Am. J. Sci.* 242, 8:417–30.
- Marsh, O. C.** 1869. Notice of some new reptilian remains from the Cretaceous of Brazil. *Am. J. Sci. (Ser. 2)* 47, 141:390–92.
- 1870. Notice of a new species of gavial from the Eocene of New Jersey. *Am. J. Sci. (Ser. 2)* 50, 148:97–99.
- 1871a. Notice of some new fossil reptiles from the Cretaceous and Tertiary formations. *Am. J. Sci. (Ser. 3)* 1, 6:447–59.
- 1871b. [A communication on some new reptiles and fishes from the Cretaceous and Tertiary formations.] *Proc. Acad. Nat. Sci. Philadelphia* 1871:103–05.
- 1872. Preliminary description of new Tertiary reptiles. Parts 1 and 2. *Am. J. Sci. (Ser. 3)* 4, 12:298–309.
- 1877. Notice of some new vertebrate fossils. *Am. J. Sci. (Ser. 3)* 14, 81:249–56.
- 1881. Principal characters of American Jurassic dinosaurs. Part V. *Am. J. Sci. (Ser. 3)* 21, 125: 417–23.
- 1882. Classification of the Dinosauria. *Am. J. Sci. (Ser. 3)* 23, 133:81–86.
- 1884. A new order of extinct Jurassic reptiles (Macelognatha). *Am. J. Sci. (Ser. 3)* 27, 160:341.
- 1890. Distinctive characters of the Order Hallopoda. *Am. J. Sci. (Ser. 3)* 39, 233:415–17.
- 1891. Geological horizons as determined by vertebrate fossils. *Am. J. Sci. (Ser. 3)* 42, 250:336–38.
- 1895a. The Reptilia of the *Baptanodon* beds. *Am. J. Sci. (Ser. 3)* 50, 299:405–06.
- 1895b. On the affinities and classification of the dinosaurian reptiles. *Am. J. Sci. (Ser. 3)* 50, 300: 483–98.
- 1896. A new Belodont reptile (*Stegomus*) from the Connecticut River Sandstone. *Am. J. Sci. (Ser. 4)* 2, 7:59–62.
- 1897. Vertebrate fossils of the Denver Basin. *Monogr. U.S. Geol. Surv.* 27:473–527.
- 1898. The value of type specimens and importance of their preservation. *Am. J. Sci. (Ser. 4)* 6, 35: 401–09.

- Matthew, W. D.** 1909. The Carnivora and Insectivora of the Bridger Basin, middle Eocene. Mem. Am. Mus. Nat. Hist. 9, 6:291–567.
- Mawson, J.** and **A. S. Woodward.** 1907. On the Cretaceous Formation of Bahia (Brazil), and on vertebrate fossils collected therein. Q. J. Geol. Soc. London 63:128–39.
- McGrew, P. O.** and **R. Sullivan.** 1970. The stratigraphy and paleontology of Bridger A. Univ. Wyoming Contrib. Geol. 9, 2:66–85.
- Mitchell, J. G.** 1957. Canon City–Colorado Springs measured section, p. 27–31. In E. D. McKee (ed.), Colorado measured sections. Denver, Rocky Mount. Assoc. Geol.
- Moody, R. T. J.** and **E. Buffetaut.** 1981. Notes on the systematics and paleoecology of the crocodyles and turtles of the Metlaoui Phosphates (Eocene) of southern Tunisia. Tertiary Res. 3, 3:125–40.
- Mook, C. C.** 1921a. *Allognathosuchus*, a new genus of Eocene crocodylians. Bull. Am. Mus. Nat. Hist. 44: 105–10.
- 1921b. Description of a skull of a Bridger crocodile. Bull. Am. Mus. Nat. Hist. 44:111–16.
- 1933. A skull of *Crocodylus clavis* Cope in the United States National Museum. Am. Mus. Novitates 678:1–7.
- 1941. A new crocodylian *Hassiacosuchus kayi* from the Bridger Eocene Beds of Wyoming. Ann. Carnegie Mus. 28:207–20.
- 1960. *Diplocynodon* remains from the Bridger Beds of Wyoming. Am. Mus. Novitates 2007:1–4.
- 1962. A new species of *Brachyuranochampsa* (Crocodylia) from the Bridger Beds of Wyoming. Am. Mus. Novitates 2079:1–6.
- 1967. Preliminary description of a new goniopholid crocodylian. Kirtlandia 2:1–10.
- Norell, M. A.** 1988. Cladistic studies in paleobiology as applied to the phylogeny of the Alligatoridae. Ph.D. dissertation, Yale University, unpublished.
- The higher level relationships of the extant Crocodylia. J. Herpetol., in press.
- Oppel, R.** 1811. Ordnungen, Familien, und Gattungen der Reptilien als Prodrum einer Naturgeschichte derselben. Vienna, M. Oettel.
- Ostrom, J. H.** 1971. On the systematic position of *Macelognathus vagans*. Postilla (Peabody Mus. Nat. Hist., Yale Univ.) 153:1–10.
- Owen, R.** 1841 (1842). Report on British fossil reptiles. Part II. Rep. Br. Assoc. Adv. Sci. 1841:60–204.
- 1849. Notes on remains of fossil reptiles discovered by Prof. Henry Rogers of Pennsylvania, U.S., in Greensand formations of New Jersey. Q. J. Geol. Soc. 5:380–83.
- Ride, W. D. L., C. W. Sabrosky, G. Bernardi, R. V. Melville, J. O. Corliss, J. Forest, K. H. L. Key and C. W. Wright.** 1985. International Code of Zoological Nomenclature, Third Edition, adopted by the XX General Assembly of the International Union of Biological Sciences. London. 338 p.
- Schuchert, C.** 1939. The geological horizon of the dinosaurs *Hallopus* and *Nanosaurus agilis*. Am. J. Sci. 237:19–26.
- Steele, R.** 1973. Crocodylia. Handb. Paläoherpetologie 16. 116 p.
- Storrs, G. W.** 1986. A dyrosaurid crocodile (Crocodylia: Mesosuchia) from the Paleocene of Pakistan. Postilla (Peabody Mus. Nat. Hist., Yale Univ.) 197:1–16.
- Swinton, W. E.** 1930. On fossil Reptilia from Sokoto Province. Geol. Surv. Niger. 13:1–56.
- Thevenin, A.** 1911. Le *Dyrosaurus* des phosphates de Tunisie. Ann. Paléontol. 11:94–108.
- Troedsson, G. T.** 1924. On crocodylian remains from the Danian of Sweden. Lunds Univ. Arsskr., N.F. 2, 20:2; Kungl. Fysiograf. Sällskapets Handl., N.F., 35, 2:1–75.
- Troxell, E. L.** 1925a. The Bridger crocodyles. Am. J. Sci. (Ser. 5) 9, 49:29–72.
- 1925b. *Hyposaurus*, a marine crocodylian. Am. J. Sci. (Ser. 5) 9, 54:489–514.
- 1925c. *Thoracosaurus*, a Cretaceous crocodile. Am. J. Sci. (Ser. 5) 10, 57:219–33.
- Van Hoepen, E. C. N.** 1915. Contributions to the knowledge of the reptiles of the Karroo Formation. Part 4. A new pseudosuchian from the Orange Free State. Ann. Transvaal Mus. 5, 1:83–87.
- Walker, A. D.** 1968. *Protosuchus*, *Proterochampsa*, and the origin of phytosaurs and crocodyles. Geol. Mag. 105:1–14.
- 1970. A revision of the Jurassic reptile *Hallopus victor* (Marsh), with remarks on the classification of crocodyles. Philos. Trans. R. Soc. London (Ser. B) 257:323–72.
- 1972. New light on the origin of birds and crocodyles. Nature (London) 237, 5353:257–63.

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- Wassersug, R. J. and M. K. Hecht.** 1967. The status of the crocodylid genera *Procaimenoidea* and *Hassiacosuchus* in the New World. *Herpetologica* 23:30-34.
- West, Robert M.** 1976. Paleontology and geology of the Bridger Formation, southern Green River Basin, southwestern Wyoming. Part 1. History of field work and geological setting. *Contrib. Biol. Geol., Milwaukee Public Mus.* 7:1-12.
- Williston, S. W.** 1905. The *Hallopus*, *Baptanodon*, and *Atlantosaurus* beds of Marsh. *J. Geol.* 13:338-50.
- Wood, H. E.** 1934. Revision of the Hyrachyidae. *Bull. Am. Mus. Nat. Hist.* 67, 5:181-295.

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